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RESEARCH ARTICLE

The interactive effects of heat stress, parasitism and host plant quality in a host–parasitoid system

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Abstract

1. Species interactions are expected to change in myriad ways as the frequency and magnitude of extreme temperature events increase with anthropogenic climate change.
2. The relationships between endosymbionts, parasites and their hosts are particularly sensitive to thermal stress, which can have cascading effects on other trophic levels.
3. We investigate the interactive effects of heat stress and parasitism on a terrestrial tritrophic system consisting of two host plants (one common, high-quality plant and one novel, low-quality plant), a caterpillar herbivore and a specialist parasitoid wasp.
4. We used a fully factorial experiment to determine the bottom-up effects of the novel host plant on both the caterpillars' life history traits and the wasps' survival, and the top-down effects of parasitism and heat shock on caterpillar developmental outcomes and herbivory levels.
5. Host plant identity interacted with thermal stress to affect wasp success, with wasps performing better on the low-quality host plant under constant temperatures but worse under heat-shock conditions.
6. Surprisingly, caterpillars consumed less leaf material from the low-quality host plant to reach the same final mass across developmental outcomes.
7. In parasitized caterpillars, heat shock reduced parasitoid survival and increased both caterpillar final mass and development time on both host plants.
8. These findings highlight the importance of studying community-level responses to climate change from a holistic and integrative perspective and provide insight into potential substantial interactions between thermal stress and diet quality in plant–insect systems.

KEYWORDS
climate change, host plant quality, parasitism, plant–insect interactions, thermal stress, tritrophic system

1 | INTRODUCTION

Anthropogenic climate change is influencing many aspects of how organisms interact within their communities (Bale et al., 2002; Gilman et al., 2010; Tylianakis et al., 2008). The increasing frequency and severity of extreme temperature and precipitation events (Portner et al., 2022) will affect organismal survival as individuals fail to withstand heat waves and cold snaps (reviewed in Filazzola et al., 2021). These events, along with changes in precipitation and other abiotic factors, will dictate species-level geographic distributions (Graham & Grimm, 1990). As species change their geographic ranges in response to climate change (Parmesan, 1996), populations may be introduced to novel biotic interactions in which the interacting members do not share a co-evolutionary history.

Environmental perturbations can change pairwise interactions, such as predator–prey (Draper & Weissburg, 2019) or plant–herbivore relationships (Massad & Dyer, 2010). These relationships become more sensitive to such disruptions when one member of the interaction is specialized (Allesina & Tang, 2012; Biella et al., 2020; May, 1972): the specialist species relies on a narrow range of conditions to survive (Clavel et al., 2011; Janzen, 1978), and any disruption can easily cause changes to the species' survival or persistence (Filazzola et al., 2020; Hassell, 2000; Ives et al., 2000; Lafferty & Holt, 2003). The relationships between endosymbionts and their hosts are particularly sensitive. Such endosymbionts are often specialists, and may have a lower thermal tolerance than their hosts (Karban, 1998; Moran et al., 2008; Zhang et al., 2019). This effect can have large-magnitude consequences when hosts are exposed to temperatures higher than their endosymbionts can survive (Thomas & Blanford, 2003); well-known examples include symbiont loss or expulsion, such as coral bleaching (Brown, 1997), and behavioural fever, like in amphibians infected with chytrid fungus (Richards-Zawacki, 2010). These thermal mismatch effects may influence further trophic levels through altered consumption of food material (Réveillon et al., 2022; Winder & Schindler, 2004) or modified pollination services (Hammer et al., 2021).

Investigating the thermal ecology of species interactions requires a study system in which both the mechanisms of interactions and the physiology and thermal biology of each species are well understood. The system comprised of the tobacco hornworm, *Manduca sexta*, and its parasitoid enemy, *Cotesia congregata*, fulfils those requirements. *M. sexta* is a model system in insect development (Nijhout, 1975; Nijhout et al., 2006), thermal biology (Kingsolver & Woods, 1997) and host–parasitoid dynamics (Beckage et al., 1994; Beckage & Riddiford, 1978), and its native range stretches across most of the Southern United States, Mexico and Latin America. *C. congregata* is *M. sexta*'s primary ecological enemy where their ranges overlap in the Southeastern United States, having been observed to parasitize between 50% and 90% of *M. sexta* larvae in the field (Kester et al., 2002; Lawson, 1959). While *M. sexta* can tolerate a broad range of temperatures, the thermal tolerance of *C. congregata* (in the egg, larval and adult stages) is lower than that of larval *M. sexta* (Agosta et al., 2018; Moore et al., 2021). The mechanism of parasitism is understood: when a female wasp oviposits into a larval host, it deposits an endogenous bracovirus as well as eggs and venom (Beckage et al., 1994). The bracovirus disrupts the host's immune and developmental pathways, lowering encapsulation and melanization responses (Amaya et al., 2005; Beckage, 1998), as well as halting development so hosts never enter the pre-pupal stage known as 'wandering' (Beckage et al., 1994). Wandering is a distinctive behaviour of normally developing *M. sexta* larvae where they stop feeding, travel off of their host plant to the soil surface and burrow into the ground to pupate (Nijhout, 1976). Parasitized *M. sexta* do not exhibit wandering behaviour (Nijhout, 1976), as their development has been arrested in the last larval instar by the bracovirus, preventing pupation (Beckage et al., 1994).

Parasitized caterpillars and the developing wasps they contain can be affected by thermal stress in several ways. Under some temperature conditions, the wasps develop successfully to emergence and eclosion; under others, the wasps die in the egg or larval stages, leaving their hosts alive (Moore et al., 2021). These hosts continue feeding during their final developmental instar and never pupate, sometimes reaching abnormally large sizes and long larval lifespans (Moore et al., 2022). While most of these caterpillars, halted from entering the pre-pupal stage by the active bracovirus, will die as these large larvae, some may even experience 'rescue', successfully recovering from parasitism enough to pupate (Malinski et al., 2023). This range of possible system outcomes—from wasp emergence to caterpillar rescue—provides a unique opportunity to use the *M. sexta*–*C. congregata* system to study the effects of thermal stress on host–parasitoid interactions.

Another factor that has been demonstrated to influence both thermal tolerance and species interactions is diet quality (Boukal et al., 2019; Laws & Joern, 2013; Vanderplanck et al., 2019). Low-quality diets can interact with an organism's ability to effectively thermoregulate (Clissold et al., 2013; Coggan et al., 2011) or lower immune responses important in defending against infection or parasitism (Lange et al., 2014; Triggs & Knell, 2012). A robust body of research describes the effects of diet quality on the larval growth and development of *M. sexta* and its interactions with *C. congregata*. Changes in nutrient concentrations (Ojeda-Avila et al., 2003), defensive compounds (de Boer & Hanson, 1987; Thompson & Redak, 2007) or host plant species (de Boer, 1992; de Boer & Hanson, 1984; Garvey et al., 2020; Yamamoto, 1974) can determine larval developmental success. Like many other Lepidopteran larvae, low-quality diet (e.g. the presence of harmful allelochemicals or the lack of necessary nutrients) can delay development, stunt growth and decrease fecundity in *M. sexta* (Yamamoto, 1960). While *M. sexta* most commonly specializes on plants in the family Solanaceae such as wild and cultivated tobacco (*Nicotiana* sp.) in the Southeast and jimsonweed (*Datura* sp.) expanding into the Southwest, individuals have been observed feeding on devil's claw (*Proboscidea* sp.: Martyniaceae) (Mechaber & Hildebrand, 2000; Mira & Bernays, 2002) in both locations. Devil's claw species *Proboscidea louisianica* has moved north into the Southeast and Mid-Atlantic from Louisiana and Florida

(Small, 1903), placing it in the same range as the *M. sexta–C. congregata* complex. Manipulative experiments have demonstrated that devil's claw is a lower-quality host plant than Solanaceous plants like tobacco because it slows larval development (Diamond & Kingsolver, 2010a, 2012), lowers masses at wandering and adulthood (Diamond & Kingsolver, 2012) and disrupts larval immune function (Diamond & Kingsolver, 2011). The reductions in development rate and final size on devil's claw are greatest at lower temperatures (Diamond & Kingsolver, 2010a).

Despite the low host plant quality for developing larvae, *M. sexta* adults readily oviposit on devil's claw in the field (Diamond & Kingsolver, 2010b). This may be because rates of parasitism by *C. congregata* on larvae found on devil's claw are significantly lower than on larvae found on tobacco (Diamond & Kingsolver, 2010b), providing an 'enemy-free space' for the *M. sexta* larvae to develop. It is currently unclear how devil's claw affects developing *C. congregata* larvae, given that the suite of defensive chemicals in devil's claw leaves is far different than those in tobacco, particularly lacking nicotine, tobacco's main defensive compound (Riffle et al., 1990, 1991). Importantly, host plant properties such as nicotine concentration are known to affect *C. congregata* developmental success at non-stressful temperatures (Kester & Barbosa, 1994); in fact, nicotine concentrations that do not affect *M. sexta* development have been demonstrated to negatively affect *C. congregata* larval development (Barbosa et al., 1991). While it is currently unknown whether devil's claw's low quality is due to a lack of necessary nutrients or the presence of unfamiliar and harmful defensive compounds, the effects of a different host plant on *C. congregata* success have not been studied (but see Thompson et al. (2005a, 2005b) for effects of artificial diet quality in parasitized caterpillars). In order to accurately model community responses to warming temperatures and the potential effects of host range expansion on higher trophic levels, the effects of host plant identity and quality must be incorporated into host–parasitoid research questions.

Here, we combine caterpillar–parasitoid and caterpillar–host plant interactions to investigate the impact of extreme temperature events and the introduction of a novel host plant (devil's claw) on the tritrophic system of *C. congregata*, its host *M. sexta* and the common host plant tobacco. We experimentally determine how parasitism, thermal stress and host plant identity combine to affect the members of the system and the interactions between them. Specifically, we ascertain (a) how host consumption of devil's claw influences *C. congregata* survival and developmental success and (b) how temperature stress interacts with this novel host plant to influence the development of *M. sexta* and the survival of *C. congregata*. We also investigate changes in *M. sexta* herbivory between the common and novel host plants.

A priori, we anticipated a reduction in the survival of *C. congregata* from caterpillar hosts that fed on devil's claw, as its lower quality cascaded upwards to affect the wasps as well as their hosts. This would manifest in two ways: (1) lower survival from emergence to eclosion on hosts fed devil's claw and (2) lower overall wasp survival on hosts fed devil's claw, as determined by lower frequencies of wasp emergence among such hosts. Also, we predicted an increase in herbivory on devil's claw across caterpillar developmental outcomes, as the caterpillars need to consume more of the low-quality resource in order to gain sufficient mass to pupate. Our experimental results outlined below confirm the expected reduction in wasp success but show the opposite trend with regards to herbivory.

2 | METHODS

2.1 | Experimental design

To investigate the interactive effects of heat stress, parasitism and host plant identity, we implemented a fully factorial design, with sample sizes weighted towards the parasitized treatment groups to account for expected mortality. Based on prior studies (Malinski et al., 2023; Moore et al., 2020, 2021, 2022), we anticipated that our treatment groups would result in several system outcomes (Figure 1): (1) In the non-parasitized, non-heat-shocked group, caterpillars would reach the pre-pupal stage known as *Wandering*; (2) In the non-parasitized, heat-shocked group, caterpillars would also reach the pre-pupal stage of *Wandering*; (3) In the parasitized non-heat-shocked group, caterpillar hosts would die upon successful *Wasp Emergence*; and (4) In the parasitized heat-shocked group, outcomes may include host death and *Wasp Emergence*, host death *Without Wasp Emergence* and host recovery of the pre-pupal *Wandering* stage. We expected that these outcomes would be consistent across host plant types.

We used caterpillar and wasp developmental events to ascertain the developmental outcome for an individual caterpillar host. The *M. sexta* pre-pupal stage is clearly categorized by increased visibility of the dorsal vein, cessation of feeding and distinctive 'wandering' behaviour that imitates digging into the soil to pupate (Nijhout, 1976). The presence of all three was required to indicate a caterpillar had reached *Wandering* successfully. Individuals exhibiting these cues in the parasitized heat-shocked group also underwent genetic testing to ensure a successful parasitism event. These individuals were frozen and tested for the presence of the endemic bracovirus using PCR (Malinski et al., 2023); all such individuals tested positive (indicating a successful wasp oviposition event and subsequent recovery of the caterpillar pre-pupal stage). Next, wasp emergence is a clearly visible event, as the wasp larvae chew their way through the host cuticle and begin to spin cocoons (Kester & Barbosa, 1991). Any number of visible wasp larvae emerged was sufficient to include the individual in the *Wasp Emergence* outcome. Finally, parasitized individuals without wasp emergence that did not exhibit the three indicators of wandering were maintained until 3 weeks after their final moult. At that point, they were removed from the experiment and classified into the *Without Wasp Emergence* outcome (Moore et al., 2021).

2.2 | Study system

In April 2020, tobacco (strain NC95) and devil's claw seeds (harvested from lab-grown plants originally sourced from Circa Plants,

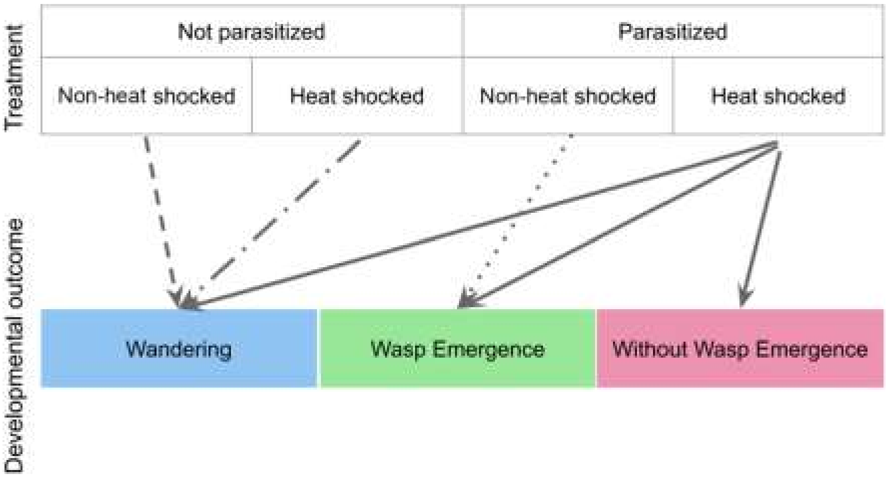

FIGURE 1 Diagram outlining the expected developmental outcomes from each treatment group. The non-parasitized treatments (both non-heat-shocked, dashed line and heat-shocked, dot-dashed line) were both expected to exhibit successful host *Wandering* since no wasps were introduced to those individuals. While all individuals in the parasitized non-heat-shocked treatment (dotted line) were expected to exhibit *Wasp Emergence*, all three developmental outcomes were possible in the parasitized heat-shocked treatment (solid lines).

lot #*prolou18a*, 2018) were germinated in environmental chambers with a 30°C, 14-h light day period and a 20°C, 10-h dark night period. Five days after sprouting, plants were transferred to the UNC-Chapel Hill greenhouse, where they remained for the rest of the experiment. They were transplanted as needed and fertilized weekly after reaching 4 weeks of age. At the start of the 6-week experimental period, both host plants were 12 weeks old.

In July 2020, wild *M. sexta* eggs were collected from organic tobacco fields in Clayton, Chapel Hill and Rocky Mount, NC. They were placed on either tobacco or devil's claw leaves and kept in a 25°C, 14L:10D light cycle environmental chamber until hatching.

Cotesia congregata individuals from the laboratory colony at UNC-Chapel Hill were used to parasitize the parasitized treatment groups. The laboratory colony was founded in 2017 from a colony at Virginia Commonwealth University (started with individuals from the Southern Piedmont Agricultural Research and Experimental Station (Moore et al., 2020)), with wild-caught individuals from eastern North Carolina added each summer to maintain genetic variation. No ethical approval was required to handle the wasps or the caterpillars.

2.3 | Rearing and data collection

After hatching, caterpillars were reared communally on fresh-cut devil's claw or tobacco leaves in a 25°C environmental chamber with a 14L:10D light cycle until the day of moult to the third instar, when they entered the experiment. Once moulted to the third instar, their masses were recorded, they were assigned an individual ID and they were placed in small individual bins with a fresh-cut leaf according to the host plant treatment group. Individuals in the parasitized treatment groups were subsequently parasitized via the laboratory colony of *C. congregata*. Then, individuals in the heat-shocked treatment groups entered an environmental chamber for a 12-h heat shock of 40°C, while the non-heat-shocked groups were placed in a different chamber, maintaining at 25°C constant. The next morning, surviving individuals were transferred into their experimental rearing conditions (consisting of divided bins housing four individuals per bin, see Figure S1), given new leaf material and stored in a temperature- and humidity-controlled walk-in chamber (25°C, 14L:10D, ~50% humidity).

Individual caterpillar mass was recorded at each moult and at their exit from the experiment (wandering, wasp emergence, 3 weeks post-final moult). The masses of caterpillars exhibiting the *Without Wasp Emergence* developmental outcome were also recorded weekly during the post-final moult period. Caterpillars were fed ad libitum on fresh-cut leaves from the host plants in the greenhouse. Leaves/leaf clusters were given individual IDs and scanned with a custom-built leaf scanner that measured leaf surface area. Specifications for the leaf scanner can be found in the supplement. Each leaf was scanned before and after consumption to allow for the calculation of the leaf area consumed. The sum of leaf areas consumed over the course of the experiment was reported as the total leaf area consumed per individual. Though leaf thicknesses and water contents differ between host plants, with tobacco leaves being thicker and containing more water (see Table S1), leaf surface area was measured due to direct ecological applicability to plant success.

When individual caterpillars exhibited wasp emergence (visible wasp larvae or cocoons on the cuticle of the caterpillar), they were placed in small condiment cups and allowed to rest for 2–3 days. Then, cocoons and emerged *C. congregata* larvae that failed to spin cocoons were removed from the host cuticle, counted and totalled as the number of wasps emerged. The caterpillar hosts' masses were recorded for their developmental outcome endpoint and culled. Wasp cocoons were transferred to a fresh condiment cup and allowed to eclose over the course of the next week. Once dead (2–3 days after eclosion), all mature, eclosed wasps were counted. The number of wasps successfully eclosed divided by the total number emerged yielded the percentage survival from emergence to eclosion for each caterpillar host.

2.4 | Statistical analyses

To determine whether observed caterpillar developmental outcomes in the parasitized heat-shock treatment differed based on host plant, a multinomial regression was performed using the *multinom* function in the package *nnet* (v. 7.3-18) in R. The base state was set to wasp emergence (normal outcome in the absence of heat stress). After fitting the model, a two-tailed *Z*-test was conducted to determine whether the proportions of observed outcomes differed based on host plant consumed (Fagerland et al., 2008).

To assess the impact of host plant on wasp success, two linear models were constructed and analysed. The first investigated the effects of host plant and temperature treatment on the number of wasps emerged from hosts with wasp emergence. The number of emerging wasps was log-transformed to reduce heterogeneity of variance. Host plant type, temperature treatment and their interaction were the predictor variables, and the test was run using the *lm* function. Next, to test the eclosion success of emerged wasps, a binomial linear regression was performed, with the proportion of wasps successfully eclosed as the response variable and host plant, temperature treatment and their interaction as predictor variables, weighted by the number of wasps emerged. This was conducted using the *glm* function, family = 'binomial'. Finally, the influence of parasitism on host mortality was analysed using another binomial regression, with parasitism status as a categorical predictor variable and survival as a binary response variable, using the *glm* function, family = 'binomial'. Analysis of variance (ANOVA) tests were conducted for each test to determine the influence of each predictor variable on the response.

To investigate the effects of temperature, parasitism and host plant on caterpillar life history, the developmental and consumption data were analysed in two different ways. First, a set of linear mixed-effects models were run using the *lmer* function of the package *lmerTest* (v. 3.1-3), with temperature treatment, parasitism status, host plant and their interactions as predictors and the experimental bin as a random effect. The second set of linear mixed-effects models utilized developmental outcome, host plant and their interaction as predictors, with the experimental bin as a random effect. For each metric of interest—maximum mass achieved, age at maximum mass and leaf surface area consumed—the two models were compared using the Akaike Information Criterion (AIC) to determine which explained a higher proportion of the variance in the data. For each response variable of interest, the models utilizing developmental outcome rather than treatment group explained a larger proportion of the variance in the data, as demonstrated by lower AIC values (age at maximum mass: ΔAIC = 80.12, maximum mass: ΔAIC = 210.02, leaf area consumed: ΔAIC = 204.95). However, for clarity, the models using treatment group are displayed (see Section 3.3). For each, an ANOVA was conducted to determine which variables significantly predicted the response. All statistical analyses were conducted using R v. 4.2.2 (R Core Team, 2022).

3 | RESULTS

3.1 | Developmental outcomes across treatments

All individuals in the non-parasitized treatments displayed the cues for *Wandering*, and all individuals in the parasitized non-heat-shocked group exhibited *Wasp Emergence* (Figure 2). The individuals in the parasitized heat-shocked treatment displayed the full range of possible developmental outcomes (Figure 2), showcasing a high level of individual variability in the response to thermal stress.

Parasitism increased caterpillar mortality, with a higher proportion of parasitized individuals dying after entering the experiment but before

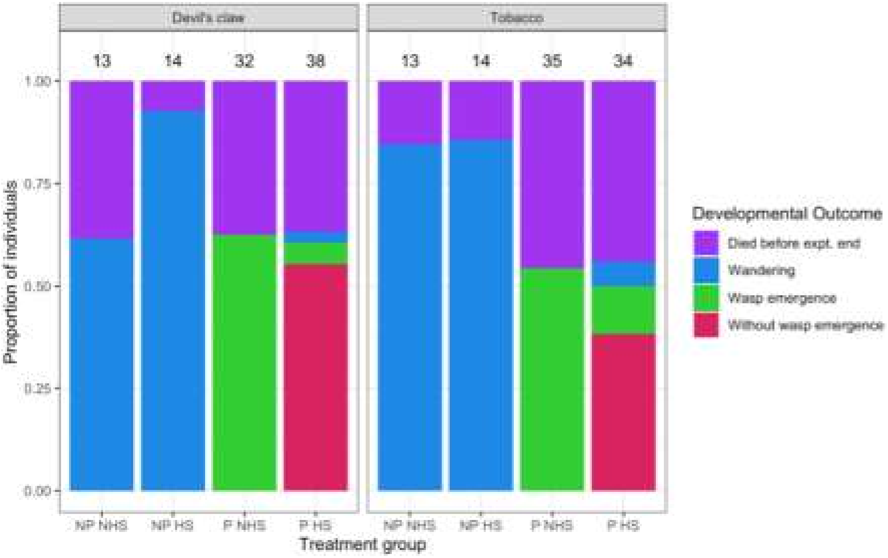

FIGURE 2 Proportion of caterpillars exhibiting each developmental outcome across treatment groups and host plant types. Total sample sizes are listed at the top of each bar. The proportions of outcomes in the parasitized heat-shocked (P HS) treatments differed slightly when feeding on the tobacco host plant (right panel) compared to devil's claw host plant (left panel).

reaching a developmental end (Figure 2, $p = 0.011$). The proportion of parasitized heat-shocked caterpillars falling into different developmental outcomes was not significantly affected by the host plant (Figure 2, $p = 0.158$). A small proportion of parasitized heat-shocked individuals for each host plant exhibited recovery of the pre-pupal wandering stage (Figure 2, blue bars), which was verified by PCR (see Section 2.1).

3.2 | Wasp emergence and survival post-emergence

The number of wasps emerging from hosts exhibiting *Wasp Emergence* (Figure 2, green bars) was significantly affected by both heat-shock treatment ($p < 0.001$) and the interaction of treatment and host plant ($p < 0.001$), but not by host plant alone ($p = 0.179$). In the parasitized non-heat-shocked treatment, more wasps emerged from devil's claw-fed caterpillar hosts, but that trend reversed in the parasitized heat-shocked treatment (Figure 3). Heat-shocked individuals from both host plants had fewer numbers of wasps emerge relative to non-heat-shocked individuals, indicating some (likely temperature-induced) mortality in the egg or larval stage (Figure 3). Host plant ($p < 0.001$), treatment group ($p < 0.001$) and their interaction ($p = 0.003$) all predicted the proportion of wasps surviving from emergence to eclosion (Table 1). However, the sample sizes of hosts with *Wasp Emergence* in the parasitized heat-shocked treatments were quite low (four caterpillars for tobacco, two for devil's claw), so this difference should be interpreted with caution. In both treatment groups, a lower proportion of emerged wasps from devil's claw-fed hosts successfully eclosed.

3.3 | Caterpillar development

Caterpillars exhibiting *Wasp Emergence* and some *Without Wasp Emergence* reached similar maximum masses, which were both much lower than those that exhibited *Wandering* (Figure 4). By contrast, some individuals *Without Wasp Emergence* reached extremely large maximum masses (Figure 4).

Caterpillars consuming devil's claw reached similar final masses as, but developed more slowly than, caterpillars consuming tobacco across all developmental outcomes (Figure 4). Due to the nature of their development, age at maximum mass was greater for hosts *Without Wasp Emergence*, and it varied greatly among them: some ceased eating soon after their final moult and lost weight over the rest of the experimental period, resulting in their maximum mass occurring before their final mass measurement (3 weeks past the final moult).

Parasitism, heat shock and their interaction all significantly predicted age at maximum mass, maximum mass and leaf area consumed (Table 2). Host plant identity and the three-way interaction between all predictors only significantly predicted age at maximum mass. Model results using developmental outcomes are reported in the Supplement (Table S2).

3.4 | Host plant consumption across developmental outcomes

Caterpillars exhibiting *Wandering* consumed twice as much as those exhibiting *Wasp Emergence* (and some *Without Wasp Emergence*),

TABLE 1 Proportion of emerged wasps surviving from emergence to eclosion across diet types and treatment groups.

	Not heat-shocked	Heat-shocked
Devil's claw	0.807 ± 0.044 ($n = 19$)	0.500 ± 0.500 ($n = 2$)
Tobacco	0.843 ± 0.052 ($n = 19$)	0.796 ± 0.157 ($n = 4$)

Note: Means and standard errors are reported, along with sample sizes of caterpillar hosts in parentheses.

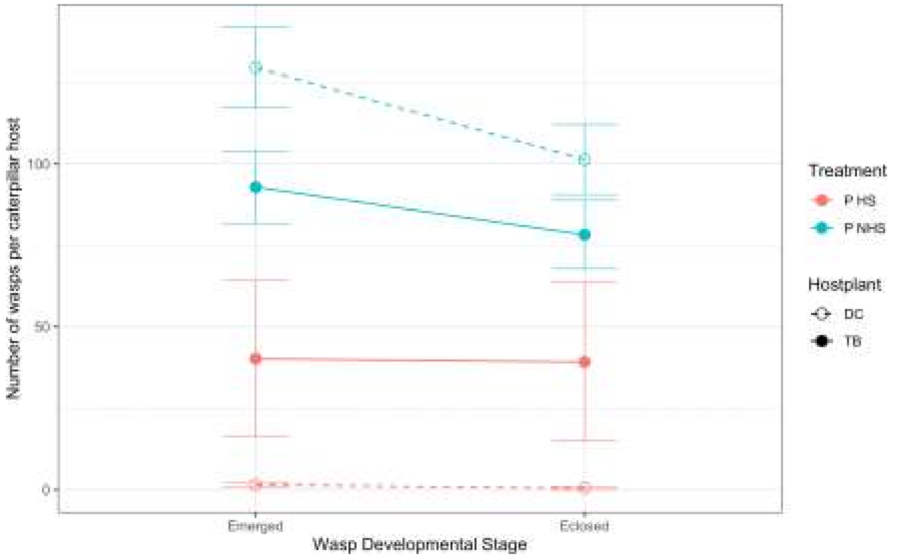

FIGURE 3 Plot showing the mean numbers of wasps that emerged and eclosed from all caterpillars, with wasp emergence across treatment groups (non-heat-shocked: blue; heat-shocked: red) and between host plants (devil's claw: open circles and dashed lines; tobacco: closed circles and solid lines). Standard error bars are shown for all groups.

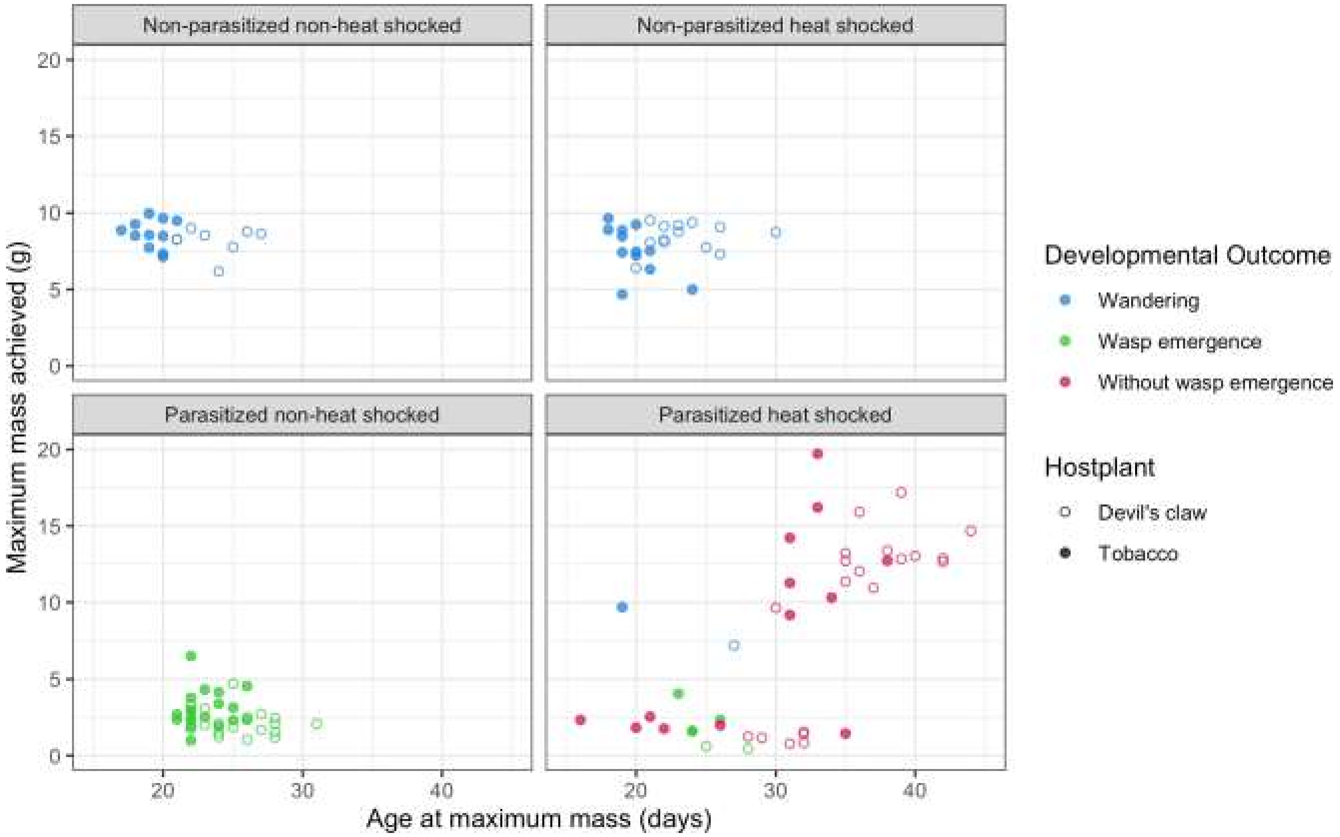

FIGURE 4 Maximum mass achieved by an individual versus development time at that maximum mass. While individuals feeding on devil's claw (open circles) and tobacco (closed circles) reached the same maximum mass within the developmental outcome, devil's claw group developed more slowly to that mass (right-shifted on the *x*-axis).

TABLE 2 ANOVA results from mixed-effect models using parasitism (abbreviated 'Para'), heat-shock status (abbreviated 'HS') and host plant (abbreviated 'Plant') as predictors.

	Age at maximum mass		Maximum mass		Leaf area consumed	
	F-value	*p*-value	*F*-value	*p*-value	*F*-value	*p*-value
Parasitism	69.8238	<**0.001**	19.6044	<**0.001**	9.0397	**0.003**
Heat shock	23.3003	<**0.001**	12.0631	<**0.001**	17.5877	<**0.001**
Host plant	38.7714	<**0.001**	0.2109	0.647	1.5042	0.222
Para:HS	20.0982	<**0.001**	16.6049	<**0.001**	11.5896	<**0.001**
Para:Host plant	0.2902	0.591	0.0236	0.878	0.4679	0.495
HS:Host plant	2.3932	0.124	1.9584	0.164	1.0681	0.303
Para:HS:Plant	4.5000	**0.036**	0.1803	0.672	0.0917	0.762

Note: Significant *p*-values are bolded.

while many *Without Wasp Emergence* consumed twice as much as *Wandering* individuals (Figure 5). Across treatment groups, caterpillars consuming devil's claw ate slightly less than, but reached the same mass as, those consuming tobacco (Figure 5). As tobacco plants have thicker leaves (Table S1), this indicates that much more tobacco material was consumed compared to devil's claw. Maximum mass achieved and total leaf area consumed were strongly associated across developmental outcomes and host plant types (Figure 5).

4 | DISCUSSION

Our experimental results indicate a complex relationship between parasitism, thermal stress and host plant identity in this plant–insect–parasitoid system. The developmental outcome achieved by *M. sexta* relies on the combination of parasitism and thermal stress, with parasitized and heat-shocked caterpillars exhibiting a wide range of masses, development times and outcomes (Figure 2). Similarly, the success of *C. congregata* depends on the interaction of host plant

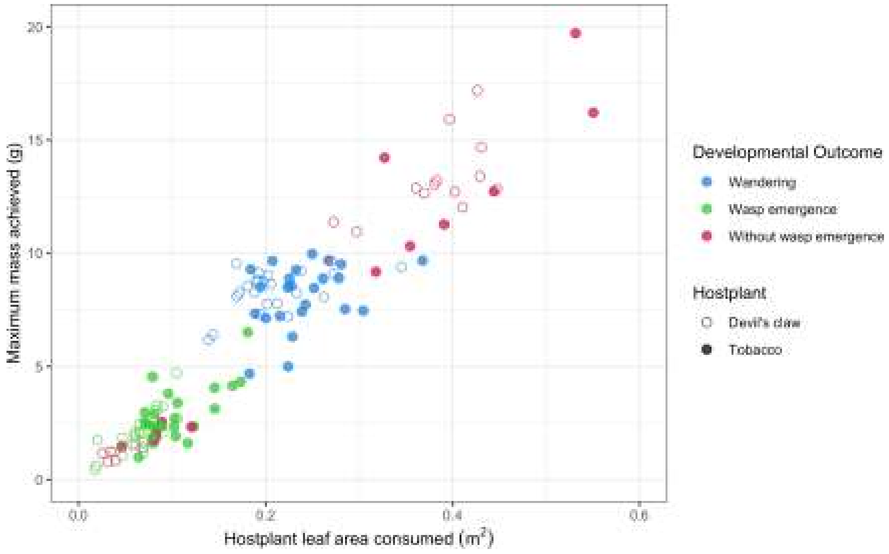

FIGURE 5 Maximum mass achieved by an individual compared to the total leaf area consumed during the experimental period. Across developmental outcomes, individuals consuming tobacco (closed circles) ate more to achieve the same mass as individuals consuming devil's claw (open circles).

identity and thermal stress (Figure 3). While herbivory was dictated by developmental outcome (Figure 5), it did not increase on the low-quality host plant as expected a priori. Below, we outline the impact of our findings in a broader ecological context, highlighting the ubiquity of such interactions in nature and the importance of multifaceted study design for predicting system reactions to global change.

4.1 | The importance of developmental variability

We observed a range of developmental outcomes in the parasitized heat-shocked treatment, indicating that the 12-h, 40°C heat shock we used was insufficient to kill all of the developing wasp eggs (whether via direct heat stress or recovered host immune function from viral disruption). In some individuals, wasps emerged successfully, while in others, they were killed so fully as to allow for host recovery of the pre-pupal stage (Figure 2). The large range of individual-level responses observed here highlights the importance of including individual variability in analyses and models, both at the herbivore and natural enemy levels. As many braconid and ichneumonid wasps exhibit similar oviposition strategies involving viral suppression of host immunity (Drezen et al., 2017), we might expect similar variability of Lepidopteran host outcomes across taxa after parasitism and heat stress.

This variability also underscores that responses to environmental stressors can vary across the range of that stressor, with certain thresholds eliciting different effects (Denlinger & Yocum, 1998; Donohue et al., 2015). While some thermal thresholds may induce mortality, others may initiate heat-shock protein synthesis or trigger winter dormancy. In this system, a lethal threshold for one interacting organism (the parasitoid wasp) triggers a different developmental outcome for another organism (the caterpillar). This concept relates back to individual variability when considering research regarding thermal acclimation and tolerance, where previous thermal history can change individual responses to stressful temperatures (Alston et al., 2020; Kingsolver et al., 2015; Marshall & Sinclair, 2012; Sinclair et al., 2003). While all caterpillars in this study experienced the same thermal conditions within treatment groups, the caterpillars' parental identity is unknown. Those individuals may have underlying genetic variation that contributed to differential immune responses (Cotter et al., 2004; Cotter & Wilson, 2002), or they may have experienced different microclimates during development, potentially leading to individualized acclimation responses in this study through transgenerational plasticity (Massamba-N'Siala et al., 2014; Mpofu et al., 2022).

4.2 | Effects of host plant on wasp and caterpillar success

We observed an interactive effect of host plant and thermal stress on wasp developmental success. Across host plants, fewer wasps emerged from heat-shocked hosts (Figure 3), likely a result of egg/larval mortality pre-emergence. While more wasps initially emerged from parasitized hosts fed devil's claw compared to tobacco in the non-heat-shocked group, the reverse was true in the heat-shocked group (Figure 3). This indicates a temperature-dependent effect of host plant identity on wasp emergence. A lower proportion of emerged wasps survived to eclosion across treatment groups on hosts fed devil's claw (Table 1). Overall wasp survival from emergence to eclosion also supports the idea of an interaction between host plant and temperature, as fewer wasps survived from parasitized hosts fed devil's claw across outcomes in the heat-shocked group (due to more individuals *Without Wasp Emergence*, and fewer wasps eclosing from those individuals exhibiting *Wasp Emergence*).

The initial emergence of more wasps from devil's claw parasitized non-heat-shocked treatment could be explained by the lack of nicotine in devil's claw leaves, a compound known to decrease wasp developmental success at high concentrations (Thorpe & Barbosa, 1986). Hosts fed on devil's claw have a reduced immune response (Diamond & Kingsolver, 2011), which could also result in higher wasp emergence. However, the reversal of this effect under heat-shock conditions may be explained by the following hypotheses: (a) the hosts recover from parasitic immunosuppression under heat stress differentially between the two host plants, resulting in more encapsulation and melanization of wasp eggs in devil's claw-fed hosts (supported by Malinski, et al, unpublished results); (b) the foreign allelochemicals in devil's claw overwhelm the hosts' processing pathways at high temperatures, exposing the wasp eggs/larvae to those chemicals and stunting growth (supported by extensive literature on negative effects of allelochemicals on parasitoids, reviewed in Kaplan et al., 2016); or (c) the slightly smaller body mass of devil's claw-fed hosts with wasp emergence (Figure 4, green points) reduced the capacity of wasp larvae to develop and eclose successfully (reviewed in Hunter, 2003). The variability of mechanisms and responses of parasitoids to host plant quality (Hunter, 2003; Kaplan et al., 2016; Sarfraz et al., 2009) invites further investigation in this system.

As expected, caterpillars that consumed more leaf material attained a higher maximum mass. Contrary to our predictions, total consumption was slightly greater on the higher-quality tobacco than on the lower-quality devil's claw, though caterpillars reached the same maximum mass on both diet types (Figure 5). This result cannot be explained by differences in water content or leaf mass per unit surface area; supplementary results indicate that devil's claw has both a lower wet and dry mass per unit surface area than tobacco, further skewing the leaf material consumed towards tobacco (Table S1). This indicates that the 'low-quality' nature of devil's claw is not explained by differences in leaf nutritional content: if devil's claw has lower nutrient concentrations or higher costs associated with processing raw leaf material, then caterpillars would need to consume more devil's claw than tobacco to reach the same mass. Instead, the differences in secondary compounds between the two plants may explain the slower consumption and growth rates and prolonged development times of caterpillars feeding on devil's claw. Previous research has demonstrated differences in feeding behaviour between *M. sexta* larvae feeding on tobacco versus devil's claw (Parker et al., 2023), resulting in fewer feeding bouts and thus slower development when reared on devil's claw. While the mechanisms of this process are still unknown, the difference in allelochemicals between the two host plants might result in longer metabolization times for devil's claw. Solanaceous feeding stimulants may also be absent from devil's claw, though no specific stimulant compounds have been identified in the current literature (de Boer & Hanson, 1987).

4.3 | Tritriophic system responses to climate change

The interactive effects described above highlight the complexity of natural systems and the difficulties in predicting community-level responses to climate change. This study demonstrates the importance of variation in host and parasitoid thermal tolerance, in host plant identity and quality and in the thermal environment itself. Our results show that one 12-h heat wave is sufficient to completely alter the dynamics of this tritrophic system, emphasizing the necessity of including natural variation in predictive models of climate change (Kingsolver et al., 2015). To fully understand the responses of systems to global change, we suggest that future research consider multiple variations of a predictor of interest—whether that be biotic (host plant, enemy, competitor) or abiotic (temperature, nutrient concentration, precipitation)—when planning manipulative experimentation.

Furthermore, our results have potentially broad-reaching implications for other host–parasitoid systems, which are often incorporated into biocontrol and agricultural practices (Wang et al., 2019). Recent work analysing longitudinal data on caterpillar–parasitoid abundance suggests declines in parasitoids with global change (Salcido et al., 2022; Stireman et al., 2005). Our results agree with the conclusions of these studies, suggesting decreases in wasp survival with frequent extreme temperature events. As braconid parasitoids are ubiquitous enemies across Lepidopteran taxa (Stireman & Shaw, 2022), we may expect similar dynamics to appear across other host–parasitoid systems. Widespread release of top-down control may cascade to important plants (especially crop species), furthering the negative effects of global warming on terrestrial communities. Research testing the ubiquity of this pattern will help the scientific community predict and respond to the effects of climate change.

AUTHOR CONTRIBUTIONS

ALP and JGK conceived the ideas and designed the methodology; ALP collected the data; ALP analysed the data; ALP led the writing of the manuscript; ALP and JGK contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code are publicly accessible on Dryad at https://doi.org/10.5061/dryad.gf1vhhmw8.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: An image of the experimental bins, where individuals were kept from the second day after moult to the third instar through the end of their developmental outcome.

Figure S2: An image of the leaf scanner with a tobacco leaf being scanned.

Table S1: Average leaf mass-to-area relationships measured for representative tobacco and devil's claw leaves ($N = 5$ for each type) prior to consumption.

Table S2: ANOVA results from mixed-effect models for development time and mass using developmental outcome as a predictor.

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